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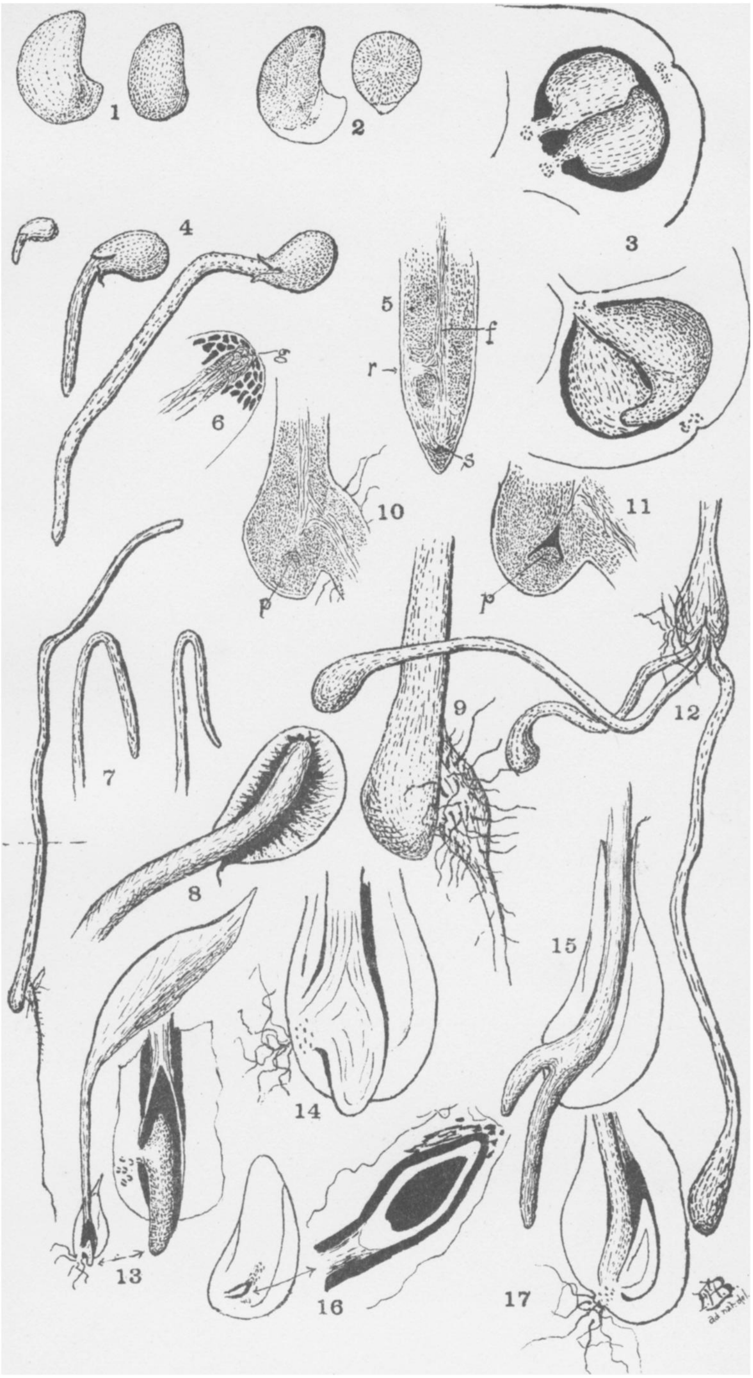

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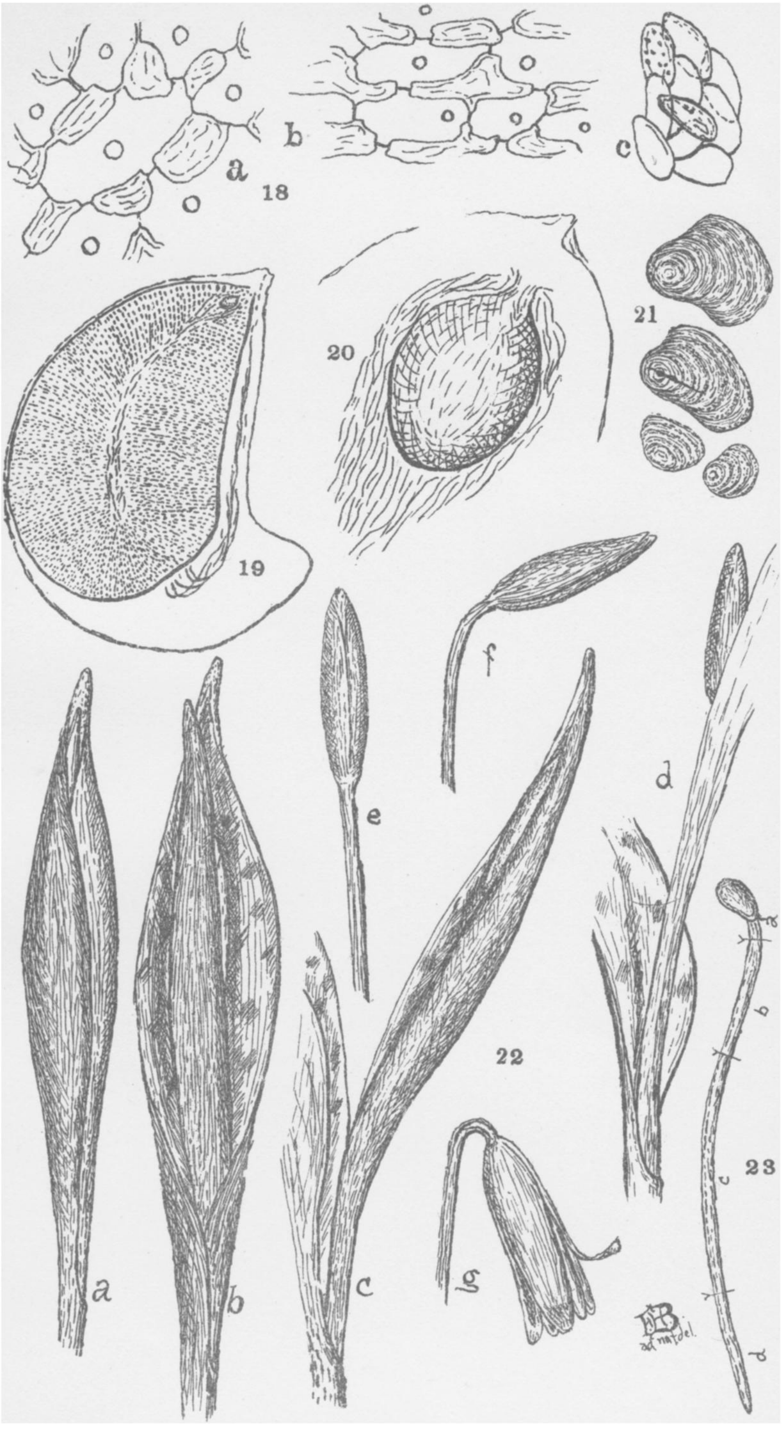

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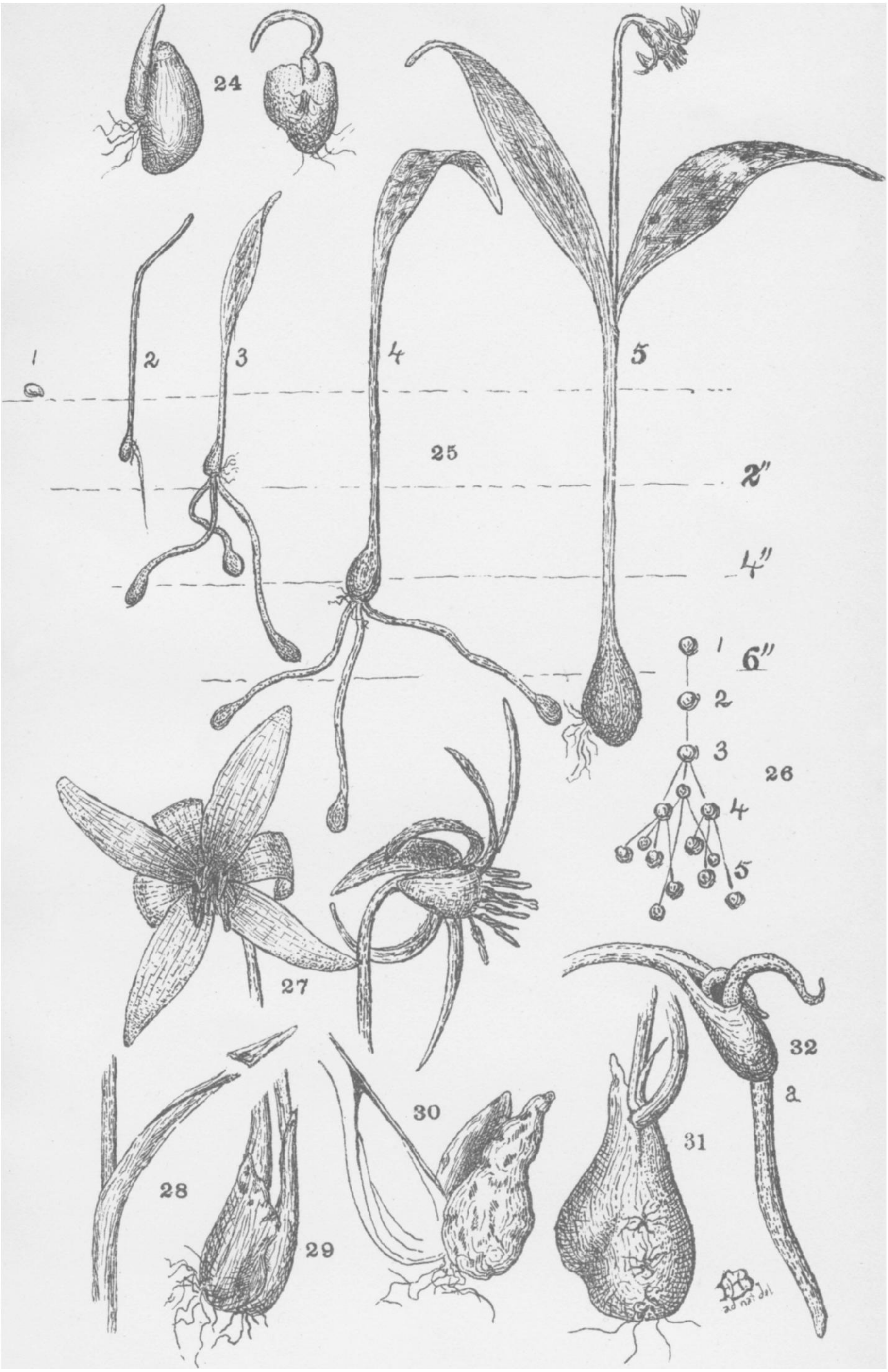

ERYTHRONIUM AMERICANUM.

Vegetative Reproduction and Multiplication in Erythronium*

By Frederick H. Blodgett

(With Plates 16–18)

John Burroughs, in Riverby, speaking of the yellow *Erythronium* as he found it in grass-covered meadows, calls attention to the brittle white threads which often appear above the turf. These he found were connected with the immature bulbs, from which they penetrate the soil in various directions.

The nature and purpose of these threads were studied in 1893 and 1894.† They are smooth, scaleless offshoots or subterranean runners, heavily charged with starch. The tip encloses a bud which will become a bulb upon the death of the parent bulb. In this species, and in *E. albidum* the runners arise from the base of the parent bulb, differing in this respect from *E. propullans* Gray, which produces the offshoots from the side of the stem above the bulb.‡

The bulbs formed at the distant end of the runners repeat the process indefinitely, producing annual crops of runners and runner-bulbs until the conditions are met which result in flowering plants. When the necessary vigor, depth and size are reached which cause the development of a flower bud in addition to the leaf bud within the bulb, the annual runners cease to be produced; but when the flowering bulb is removed from those conditions, runners are again produced. The runners are first produced from the bulbs which are formed during the growth of the seedling; the last crop gives rise to flowering bulbs four years or more after the seed has ripened. After the runners cease to be produced, annual bulbs are formed within the mature bulb, resembling the runners in their structure save that there is no lengthening between the terminal bud and the point of origin.

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* Read in abstract before the Society for Plant Morphology and Physiology, New Haven, Dec. 27, 1899.

† Bot. Gaz. **19**: 61. 1894; and **20**: 172. 1895; with illustrations.

‡ Am. Nat., July, 1871. A new Species of *Erythronium*. Dr. Gray mentions also the function of the offshoots in the species *Dens-canis*, *Americanum* and *propullans*.

The mature bulbs are usually in good flower about the middle of April, and the seeds ripen in June. They must be looked for among the leaves upon the surface of the ground, as the entire plant becomes withered and prostrate soon after the fall of the flowers. The ripe seeds are about 6 mm. long, half as wide, and in shape resemble, distantly, a segment of an orange, on account of a prominent raphe and spur along one side (Fig. 1). In texture the seed is firm and hard; in color, brown darkening with age and exposure. The surface is strongly convex, and smooth, though hardly shining. The raphe and spur are absent in seeds which have lain in the soil over winter. In *Erythronium Dens-canis* the raphe is less developed, the spur is present as a slender curved hook or beak from the apex of the seed.*

The seeds remain dormant for nine months—from June to April, when they germinate (Fig. 4), reaching their best development as seedlings (Fig. 7), about the time that the flowers are in their prime. The young plant elongates in opposite directions: the upper end, the tip of the cotyledon, contains a gland (Fig. 6, *g*) by which the food substance of the seed is absorbed. The lower end is protected by a root cap during the first stage of its growth. While the tip of the cotyledon advances the length of the seed, the opposite end penetrates the soil for an inch or more. About the time that the food is absorbed from the seed and the cotyledon frees itself from the empty testa, the descending part changes also. From one side of this portion, close to the tip (*r*, Fig. 5), the radicle is produced, and penetrates farther into the soil. It is plentifully supplied at its base with root hairs (Fig. 9).

The cotyledon is supplied, for the greater portion of its length, with stomata, and functionally it is a cylindrical leaf. Starch is scattered through it, being in all portions of the tissue at *a* (Fig. 23), mostly epidermal in the guard cells of the stomata at *b*, usually near the fibrovascular bundles at *c*, and general again at *d*. Close to the tip (*d*) there is a local deposit of starch, as if provided for the growing cells just within the root cap (*S*, Fig. 5). The part from which the radicle springs enlarges, becomes charged with starch, and forms a bulb (Fig. 9), which is usually forced deeper into the soil at the end of a short vertical runner, but may develop without such elongation. Within this bulb the plumule is formed (Figs. 10, 11) and with its formation the first step in the vegetative life of the plant is completed. The second step appears the next spring with the first leaf—the plumule leaf, and ends when the first crop of runner bulbs is formed in May.* From the plumule-bulb only one or two runners are generally produced, but from the larger bulbs three is the more common number (Fig. 12), thus increasing three-fold the number of immature bulbs at each successive crop of runners.

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*Irmisch: Beiträge zur verg. Morphologie der Pflanzen. Abhand. d. Natur. Gesell. zu Halle, 17^3: 184-195. 1863.

A flowering bulb cannot be produced from seed in less than four years. In the first year the parent bulb would bloom, and ripen its crop of seeds, from six or seven to twenty or more. In the spring of the second year some of these seeds would germinate and form plumule-bulbs. From each of the plumule-bulbs there would appear in the third year a single leaf, and the first runners would be produced at the distant ends of which runner-bulbs would be formed. Some one of these runner-bulbs might be formed under the conditions necessary to produce a flowering bulb, but this is very unlikely; so that one or more years would elapse before a blossom would be formed, thus making a cycle of five or more years. This cycle is shown at Fig. 14, with the forms assumed at each step. At Fig. 26 the multiplication which takes place during the same cycle is shown diagrammatically: one seed; one seedling and plumule-bulb; one runner bulb; three runners with their bulbs; and from each of these three there are produced three more the fifth year, nine in all. Some of the nine will probably produce a flower; those which do not will continue to produce runners in most cases, although a bulb is occasionally found which is apparently recuperating, for the depth is that of the mature bulbs, but only one leaf is produced, and no runners are present.

The following table illustrates the number of plants of different ages during each of five years, supposing that five seeds from each fruit ripen and survive the cycle. Each step is one line lower than the next preceding one, thus the five "seeds" of 1899, become "5 plumule-bulbs" in 1900, giving a total of 75 plants in 1903.

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* No bulbs of plumule size were found this spring (1900) with runners. The stiff clay soil in which most of them were found may have some influence upon the absence of runners.

1899	1900	1901	1902	1903
5 seeds	5 seeds	5 seeds	5 seeds	5 seeds
	5 plumule-bulbs	5 plumule-bulbs	5 plumule-bulbs	5 plumule-bulbs
		5 yearlings	5 yearlings	5 yearlings
			15 2 years old	15 2 years old
				45 flowers
			Total	75 plants

There is very little chance that there will be forty-five blossoms at the end of five years, but as some of the bulbs will probably flower then it is convenient to call the entire number by one name, when they are of the same crop or age.

The seed resembles that of *Iris* in structure.* The walls of the cells are thickened; at certain points the walls of adjacent cells retain their normal thin nature, so that a thin membrane only separates the cell cavities. The cells are arranged with their longer axes nearly perpendicular to the surface of the seed, and in this way form lines which extend to the central portion of the endosperm. Through the center of the seed a mass of dense reserve cellulose extends (Fig. 19) with a few cell cavities scattered through it. In the apex of the seed, and at the beginning of this mass of dense material lies the embryo (Fig. 20). At germination the embryo elongates, pushing the tip of the cotyledon along the center of the seed, absorbing the dense cellulose as it advances. From the cavity thus formed in the center, the solvent action extends toward the surface of the seed, following the lines of the cells, and producing a honey-comb effect (Fig. 8). This honey-combing is the more easily produced on account of the cell arrangement which in a longitudinal section appears as in Fig. 18, *a*; in a horizontal one, as at *b*. The thin wall separating the depressions in the thickened walls of adjacent cells readily dissolves under the action of the absorbing gland of the cotyledon, thus opening a passage for the movement of food materials from cell to cell, as the solvent action extends. The dissolved material moves along the channels so made toward the tip of the cotyledon. The absorbing organ (Fig. 6, *g*) is quite similar in structure, and probably in action also, to the glands in the hairs of *Drosera*.* One or two layers of cells cover the end of the fibro-vascular bundle which is slightly larger than in the body of the cotyledon. No starch is present in the seed, except in the raphe and spur, where a few grains are scattered through the thin-walled cells (Fig. 18, *c*). During the growth of the seedling starch is found just within the glandular tip of the cotyledon, and in other portions as already stated.

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* Haberlandt, Pflanzen Anatomie, 298.

When the food material has been exhausted the cotyledon "elbows" its way to the surface and functions as a leaf. At this stage it resembles an onion seedling, but unlike the onion no further development of foliage occurs until a year later. The plumule-bulb is now forming and is complete, as a bulb, about the time the seedlings wither early in May. The plumule is formed at the base of the swelling at the origin of the radicle (*p*, Fig. 10). At first a mere line of division separates the plumule cells from the other cells of the young bulb. Later the plumule appears as a protuberance at the bottom of a small cavity in the base of the bulb (*p*, Fig. 11). After the cotyledon withers the plumule continues to develop, until a small leaf is formed by the first of November. The plumule-bulb becomes heavily charged with starch early in its development, and thereafter the subterranean portions, except the shoots inside the bulbs are starch bearing.

Runners have their origin at the base of the stem, as a bud in the axil of the inner bulb-scale. From this point (Figs. 13, 15) they push out irregular distances, and at the completion of their growth form bulbs from their terminal buds. Mature bulbs are annually renewed from similar buds (Fig. 17), which develop inside of the parent, beginning as buds in December; the new bulb being full size just after the blossoms fall, in late April. Fig. 30 shows the new bulb at the time that the parent is in prime flower.

The runner and annual bulbs begin to form the buds for the next spring's leaves and flowers, in May. The first evidence is a discolored line or streak extending upward from close to the bottom of the bulb; soon there appears a cavity at the lower end of this streak, in which a short sprout is visible in June or July (Fig. 16). This sprout continues to develop until in November and

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* Kerner, Nat. Hist. of Plants, **2**: 145. *f. 126*.

December the floral parts are all present and well developed including the ovules and the pollen mother-cells, and the perianth is often tinged with yellow. As the spring advances the bulbs push their sprouts further and further toward the surface, and when the frost is fairly out of the ground the short distance remaining is quickly passed, and the flowers open while there may still be snow on shaded hillsides. The sprout penetrates the soil in the manner of an awl, piercing leaves and decayed wood which may lie in its path,* rather than growing around, or lifting them. For this awl-like work the sprout is protected by a hard tip, which forms the apex of the leaf when the latter expands.

In Fig. 22 the successive steps are shown, by which the flower becomes freed from the enclosing leaves, and assumes its nodding position on the pedicel. At the left (*a*) the sprout has fully penetrated the soil and the leaves have begun to relax their tight clasp upon the bud. The outer and larger leaf expands gradually, while the inner one remains close to the bud as shown at *b*. Next the two leaves bend downward toward their final position, the bud still held by the margins of the inner leaf, *c*. When the leaves have reached nearly their normal position, the bud is released *d*, and it then stands erect between the leaves, as at *e*. In a short time the stem begins to bend near the bud, as at *f*, and as the bud begins to open it has assumed the position shown at *g*.

The last two positions alternate while the plant remains in flower, position *f* being assumed on bright days, when the open flower, with strongly recurved petals, is turned upward, returning to the nodding position at night and on less warm or less sunny days. With the fall of the flower the enlarging fruit assumes an erect position upon the stem, which is retained until the whole plant is withered and lies prostrate on the ground; the ripe seeds remain quite close to the open capsule.

Erythronium Americanum in its mature development normally bears two unequal leaves and a single flower. During the past two or three seasons a number of unusual cases have been observed, in one of which two flowers were borne on an otherwise normal plant. More frequently one leaf only was present in a plant otherwise normal. Over a dozen plants showing the latter form of variation were found in an hours' collection in New Jersey. A plant collected at Washington, D. C., had one leaf (Fig. 28) eight stamens and seven petals; the flower is shown at Fig. 27. Plants having three leaves, with one flower; and four leaves, with two flowers; have been found at long intervals. Fig. 31 shows also three rosettes formed by the root fibers, which indicates the minimum age of the bulb at the depth at which it was found, that is, three years.

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* Bessey, C. E., A vegetable Awl, Plant World, 1 :. 132.

Bulbs and runners also have unusual developments, such as surface buds or stimulation growths. The latter seems to have started after a rain or other stimulation, and bursting through the partly formed runner bulb, has grown further into the soil. Fig. 31 shows one in which the nearly formed bulb is burst in two directions, sending a continuation downward, and attempting to produce leaves through the upper opening. These rudimentary leaves showed a trace of yellowish green when first gathered. In bulbs which have been injured, so that the sprout from the center of the bulb fails to develop, a surface bud may be formed. Two such bulbs were recently observed and are illustrated at Fig. 24.

The starch which is very abundant in the bulbs is very finely banded, the fine lines being accompanied at intervals by coarser ones. Fig. 21 shows some of the more common shapes assumed by the starch. Occasional grains are found which are greatly elongated. Often there is a crack or fissure running through the nucleus of the grain but this is not constant, especially in small or medium sized grains.

So far as known, a satisfactory explanation of the common name of *Erythronium* has not been given. Many plants have for their common names the translation of their Latin designation, and the common name will remain through many changes in nomenclature of the scientific descriptions. People seeing in a new country a plant closely resembling one familiar near their homes, usually give the new plant the name of the one already known. Hence when *Erythronium Americanum* was seen, so closely resembling the European species, it received the common name of hat better known plant, dog's-tooth violet.

In the library of the U. S. Department of Agriculture at Washington, there is a copy of Leonard Fuchs' herbal: De historia stirpium insignes * * * Basileae, 1542. When examining this and several other volumes in December, 1897, a description, and excellent illustration were found of the European *Erythronium*, named *Viola Dens-canis.* The *Viola* part of the name is probably due to coincidence in time and place of flowering: *Dens-canis* refers either to the shape of the bulbs, or to the dentations at the base of the petals. In another part of the same volume a number of violets are figured bearing the generic name *Viola* as now.

During the examination of old botanical works in the search for the above reference the following names were found, applied to what has been known since Linnaeus as *Erythronium Dens-canis.*

Pliny: (Historia Mundi; Froben, ed. Basillae 1554), lib. 26, ch. x., p. 472, speaks of "another *Satyrion* (called *Erythriacon*), seeds like *vitex* but larger, smooth; root hard, cortex red, enclosing white within; sweet juice; occurring in mountains."

Dioscorides (Pedacii; Saracenius, ed. 1598), lib. 3, ch. 144, p. 232.

"*Satyrion Erythronium* or *erythraicum* has seeds resembling *linum*, but larger, firm, shining or dull. * * * The cortex of the root rather delicate, and red; the internal portion white, juice sweet, pleasant to the mouth."

Dodoen's Erundeboeck, Antwerp, 1554, gives an illustration of *Satyrion erythronium*, which is probably meant to be one of the *Alliums* as some of the herbalists consider that *Allium ursinum* is referred to by Dioscorides' *Satyrion erythronium.*

Camerarius' Kreuterbuch, Frankfort, A. M., 1586, page 389. In this herbal *Hermodactylus* and *Pseudohermodactylus*, are figured side by side and represent *Iris* and *Erythronium* respectively. The two names are often given by the old botanists as synonyms of *Dens-canis*, or dog's-tooth, as they most frequently called it.

"*Pseudohermodactylus* is a beautiful plant, it brings two, or rarely three leaves much like the lily. It is spotted with many brown spots. Its flower grows upon a yellowish-brown stem, light purple with brown stamens (fasemen) and a white pistil (stiftlin), in the center. The little leaves [petals] unfold when the sun shines warm upon it, but when, however, they have fallen away, a three-angled knob develops full of yellow seeds. The root is longish, thicker below than above, which are often clustered together. * *

While it does not bloom it brings only one flower. It is called Dentali by Apotheckers in Stiermarck."

In Lobelius' Stirpium, Antwerp, 1576, there is a good cut on page 64 of *Erythronium* with the brief description : "*Erythronium* with colored flowers and unequal leaves." *Satyrion Dens caninus*, *Hermodactylus* and *Pseudohermodactylus* are given as synonyms used in different regions. "* * * Flowers either purple-red or white, or purple and white mixed."

Plunkenetius (Phytographia, 1692, **3**: 130).

"*Dens caninus*, flowers yellow, *Virginianus*." *

Salmon's Herbal, 1710.

"Dogs tooth * * * the same as 'satyrion having red cortex on the root,' in Dioscorides, lib. 3, ch. 144." Three color forms are described having white, red and purple flowers respectively.

Roberto Morrison, of London, in his Plantarum Historia Oxonienis, 1715, page 343, says that the name "*Dens canis* is from the shape of the oblong tuberous root imitating the figure of a dog's tooth, the name is good." "It has a capsule of three distinct valves. * * * When the flower is red the leaves are red spotted, when white the spots are milky."

Gronovius (Flora Virginica, 1739, 151, 1st edition).

"*Erythronium*, leaves oval or oblong, glabrous, dark-spotted, flowers yellow." † (Cited in Linnaeus Spec. Pl. 1753, as var. γ, under *E. Dens-canis*).

Gronovius' Flore Virginia, Lugdonum, 1762, 51 (2d edition), contains a description of our native species. "*Erythronium* with ovate oblong leaves, smooth, dark-spotted. *Dens-caninus aquatalis*, flower yellow, pendulous, leaves ovate-oblong, prostrate, two upon a stalk, glabrous, dark-spotted. Blooming toward the end of March."

The reproduction by offshoots or runners, is mentioned in Miller's Gardener's Dictionary, London, 1754, Vol. I., "*Dens-canis* —Dog's tooth. * * * These plants are propagated by seeds, as also by offsets from the old roots. * * * The offsets, which these plants produce but sparingly, should be taken off at the time that the old roots are transplanted, * * * toward the latter end of May."

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* *Virginianus* is italicized, as are authors cited on the same page, but here it may be a typographical error for a reference to Virginia, since the European form has purple or red flowers.

† This is probably the first description of the American species; especially interesting, as it has the modern genus name. See previous note.

Linnaeus cites descriptions from a number of the early botanists, giving them as synonyms of his *E. Dens-canis*, or as varieties of it. Thus Dodonaeus (Stirpium historiae pemptades, 1616, 203) gives "*Dens caninus*" which Linnaeus regards as synonymous with *Erythronium Dens-canis*, as is also "*Dens-canis* with broad and rotund leaves," of Bauhinus (Pinax, Basiliae, 1671). But "*Dens-canis* with narrow and elongated leaves," of the same author is regarded as variety β under *E. Dens-canis*, and Gronovius's description given in a preceding paragraph, is ranked as variety γ in Species Plantarum, 1753.

Among names used or proposed for use as non-Latin designations of *Erythronium*, Trout Lily and Fawn Lily, have been suggested by John Burroughs in Riverby, on account of the spotted leaves, and because of the alert position which the two leaves often assume. Spring Lily has been proposed, on account of its early flowering, and the lily-shaped blossom. But as a colloquial name, "Roosters" is the least suggestive of the plant meant. This name is used in central New York, among the children especially, because of the custom of "fighting roosters" with the nodding flowers or buds, as is done with violets in New Jersey.

Explanation of Plates

PLATE 16

1. Surface of ripe seeds, June and March, × 3.
2. Longitudinal and cross sections of seed (June), × 3.
3. Cross sections of ovary, April and May, × 12 and × 5.
4. Successive steps in germination, × 1½ and × 3.
5. Longitudinal section of tip of seedling. *f*, fibrovascular bundle. *r*, point of origin of radicle. *s*, deposit of starch.
6. Tip of the cotyledon, showing the absorbing gland, × 10.
7. Full grown seedlings and "elbows," × 1.
8. Tip of cotyledon in partly absorbed seed, × 6.
9. Base of cotyledon showing the enlarged portion which becomes a bulb (plumule-bulb), × 5.

10, 11. Sections of young plumule bulb, plumule at *p*, × 5.

12. Runners, and the developing runner bulbs, × 1½.

13–15. Axillary buds, from which runners will develop. Slightly enlarged.

16. The first stages of the flower-and-leaves shoot (July 1).

PLATE 17

17. Bud of annual bulb (May), × 1.

18. Three sections of seed tissue. *a*, longitudinal. *b*, transverse of endosperm. *c*, cells from raphe, containing scattered starch grains.

19. Longitudinal section of seed, × 15.

20. Embryo in endosperm, × 50.

21. Starch grains from bulb, × 225.

22. Successive steps in the liberation and orientation of the flower, × 1.

23. Seedling, showing the starch-bearing regions, × 1.

PLATE 18

24. Surface buds on bulbs after the sprouts have been destroyed, × 1.

25. Life cycle of five years, showing the successive forms assumed.

26. Diagrammatic life cycle, showing multiplication of one seed in five years.

27. Abnormal flower, petals, 7; stamens, 8; leaf, 1 (Fig. 28).

28. Leaf of 27.

29. Abnormal bulb, twinned by surface bud, × 1.

30. Annual bulb turned aside to show the relation of old and new growth.

31. Mature bulb which has been three years in one place, rosettes of root fibers indicate the age, × 1.

32. Stimulation growth of runner, × 1.